



THE UNIVERSITY *of* EDINBURGH

Edinburgh Research Explorer

Prenatal maternal effects on body condition score, female fertility, and milk yield of dairy cows

Citation for published version:

Banos, G, Brotherstone, S & Coffey, MP 2007, 'Prenatal maternal effects on body condition score, female fertility, and milk yield of dairy cows', *Journal of Dairy Science*, vol. 90, no. 7, pp. 3490-3499.
<https://doi.org/10.3168/jds.2006-809>

Digital Object Identifier (DOI):

[10.3168/jds.2006-809](https://doi.org/10.3168/jds.2006-809)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Publisher's PDF, also known as Version of record

Published In:

Journal of Dairy Science

Publisher Rights Statement:

© American Dairy Science Association, 2007

General rights

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.



Prenatal Maternal Effects on Body Condition Score, Female Fertility, and Milk Yield of Dairy Cows

G. Banos,^{*1} S. Brotherstone,^{†‡} and M. P. Coffey[†]

^{*}Department of Animal Production, School of Veterinary Medicine, Box 393, Aristotle University of Thessaloniki, GR-54124 Thessaloniki, Greece

[†]Sustainable Livestock Systems Group, Scottish Agricultural College, Bush Estate, Penicuik, Midlothian, EH26 0PH, United Kingdom

[‡]School of Biological Sciences, University of Edinburgh, Ashworth Laboratories, King's Buildings, Edinburgh, EH9 3JT, United Kingdom

ABSTRACT

In this study, maternal effects were described as age of dam at first and second calving, first-lactation body condition score (BCS) of the dam during gestation, and milk yield of the dam. The impact of these effects on first-lactation daughter BCS, fertility, and test-day milk yield was assessed. The effect of milk yield of dam on daughter 305-d yield in the latter's first 3 lactations was also investigated. The proportion of total phenotypic variance in daughter traits accounted for by maternal effects was calculated. Dams calving early for the first time (18 to 23 mo of age) had daughters that produced 4.5% more first-lactation daily milk, had 7% higher BCS, and had their first service 3 d earlier than cows whose dams calved late (30 to 36 mo). However, daughters of dams that calved early had difficulties conceiving as they needed 7% more inseminations and had a 7.5% higher return rate. Cows from second calvings of relatively young (36 to 41 mo) dams produced 6% more first-lactation daily milk, had 2% higher BCS, and showed a significantly better fertility profile than cows whose dams calved at a late age (47 to 55 mo). High maternal BCS during gestation had a favorable effect on daughter BCS, nonreturn rate, and number of inseminations per conception. However, it was also associated with a small decrease in daughter daily milk yield. Changes in dam BCS during gestation did not affect daughter performance significantly. Maternal effects of milk yield of the dam, expressed as her permanent environment during lactation, adversely affected daughter 305-d milk, fat, and protein yield. However, although the effect was significant, it was practically negligible (<0.3% of the mean). Finally, overall maternal effects accounted for a significant proportion of the total phenotypic variance of calving interval ($1.4 \pm 0.6\%$) and nonreturn rate ($1.1 \pm 0.5\%$).

Key words: maternal effects, fertility, body condition score, milk

INTRODUCTION

Early fetal development in most animal species is influenced by exogenous factors related to the uterine environment in which they are born. Such factors may include nutrient intake and partitioning by the dam, nonnuclear genomic functions, hormones, antibodies, placental permeability, and maternal behavior, and are referred to, collectively, as prenatal maternal effects (for a review, see Mousseau and Fox, 1998). They can be viewed as the uterine environment a dam offers to her fetus comprising her own genetic and environmental components, while excluding any genetic effects the dam transmits directly to the fetus.

The impact of prenatal maternal effects on postnatal development and adult life of the offspring has not been documented as well as that of postnatal nursing environment (Rutledge et al., 1972; Rhees et al., 1999). Prenatal uterine environment has been shown to have an effect on murine growth, mature size, and morphology (Cowley et al., 1989; Rhees et al., 1999). Barker (1992) speculated that nutrition of the fetus in early gestation may influence its fitness as an adult. In the Netherlands, during the winter of 1944–1945, humans were subjected to starvation rations and subsequent offspring were found to be at increased risk of coronary heart disease depending on the stage of their mothers' pregnancy when restricted nutrition had been imposed (Roseboom et al., 2000). In sheep, the nutritional state of the ewe during gestation seems to have an impact on the offspring's future reproductive performance (Gunn et al., 1995; Borwick et al., 1997). For a review of the intergenerational effects of fetal programming, see Drake and Walker (2004).

In dairy cattle, calves are removed from their dams immediately after calving; hence, any maternal effect on the calf would be a combination of prenatal uterine environment and cytoplasmic inheritance. Maternal

Received December 4, 2006.

Accepted March 20, 2007.

¹Corresponding author: banos@vet.auth.gr

lineage, implying cytoplasmic (mitochondrial genetic) effects, may account for a small but significant proportion of the variation in future offspring milk production (Schutz et al., 1992; Albuquerque et al., 1998). Jamrozik et al. (2005) reported sizeable proportions of the total variation in reproduction and fertility traits of Canadian Holsteins being due to overall maternal effects. Small but significant maternal effects on Norwegian heifer performance were reported by A.-Ranberg et al. (2003).

Very few studies have been conducted on the effect of the prenatal uterine environment on adult traits of the calf. Pryce et al. (2002) investigated the effect of maternal diet during gestation on heifer fertility but found no significant associations. However, this was attributed mainly to the lack of sizeable variation in the nutritional status of the pregnant cows raised on the research farm where that study was conducted.

A pregnant cow's capacity to care for her embryo is largely determined by the way she partitions nutrients to support fetal development together with her own growth, maintenance, and milk production. Although the energy requirements of a developing embryo at the blastocyst stage may be very small, the maternal uterine environment of a high-yielding cow may create an effect on her offspring via hormonal or other routes that are detectable in the offspring's own life through a number of traits such as milk production, disease resistance, survival, BCS, body energy, and fertility. Conceptually, a dam's own energy level may be deduced from her BCS, milk production, and age at calving. These can be viewed as indicators of maternal environment during gestation. For example, BCS is associated with the amount of energy available to sustain growth, production, and fetal development. Milk yield is the main competitor of the fetus for nutrients and energy. Age at calving manifests the state of development of the dam during gestation regarding her own growth. Fuerst-Waltl et al. (2004) reported a significant association of age of the dam with milk production and longevity of the offspring.

The objectives of this study were a) to investigate the impact of the dam's age at calving, BCS and milk yield on offspring BCS, fertility, and milk production traits and b) to estimate the maternal variance component for these traits.

MATERIALS AND METHODS

Traits of interest were mainly first-lactation BCS, measured on a scale from 1 (thin) to 9 (fat) according to Jones et al. (1999), calving interval (CI), interval between calving and first service (DFS), number of inseminations per conception (NINS), nonreturn rate at

Table 1. Descriptive statistics of first-lactation cow traits

Trait ¹	Mean	SD	Minimum	Maximum
BCS ²	4.40	1.65	-1.5	10.5
CI, d	401.7	57.4	301	599
DFS, d	87.0	31.6	3	200
NINS, n	1.74	1.08	1	10
NR56	0.67	0.47	0 ³	1
MY3, kg	26.5	5.9	5.0	59.8

¹CI = calving interval; DFS = interval from calving to first service; NINS = number of inseminations per conception; NR56 = nonreturn rate 56 d post first insemination; MY3 = daily milk yield on third test-day.

²Standardized according to Brotherstone (1994).

³0 = cow returned to service within 56 d.

56 d post-first insemination (**NR56**), and milk yield on the day of the third test (**MY3**). These traits are routinely considered in a hexivariate analysis for the computation of official national genetic evaluations for cow fertility in the United Kingdom (Wall et al., 2003a). Records were obtained from the UK national fertility database and were first validated according to Kadamdeen and Coffey (2001). The total number of fertility records was 228,229, spanning the calving year period 1997–2005. Table 1 describes these 6 traits.

Four separate studies were conducted to investigate the impact of maternal effects on these traits, considering i) the effect of calving age of the dam on offspring performance, ii) the effect of BCS of the dam during gestation on offspring performance, iii) the effect of milk yield of the dam on offspring performance, and iv) the proportion of the total variation in offspring traits due to the dam. The UK national genetic evaluation model for MY3, BSC, and fertility traits (Wall et al., 2003a) provided the base model for these analyses. Additional effects fitted were those whose impact the present study had set out to investigate, as described next. In all cases, REML variance component and effect solutions were calculated with the ASREML software package (Gilmour et al., 2002).

Age of Dam at Calving

Pairs of dams and daughters with validated fertility records were obtained from the UK national database used for fertility genetic evaluations. Daughters were from the first 2 recorded calvings of each dam. There were 13,703 first-calving records in which the average dam age was 27.4 mo (standard deviation = 3.25 mo). Based on its distribution, age at first calving was divided into 3 classes: 18–23 mo (early first calvings), 24–29 mo (intermediate first calvings), and 30–36 mo (late first calvings). There were also 11,269 second-calving records with average dam age of 39.8 mo (standard

deviation = 3.83 mo). In this case, age was divided into 4 classes: 30–35 mo (early second calvings), 36–41 mo (early-intermediate second calvings), 42–46 mo (intermediate-late second calvings), and 47–55 mo (late second calvings). The impact of age class of the dam on the daughter traits of interest was assessed with the use of the following model; separate analyses were conducted for first and second calvings:

$$Y_{ijkm} = HY_i + M_j + A_k + a_1 \cdot age + a_2 \cdot phol + a_3 \cdot mlkc + a_4 \cdot dim + a_5 \cdot bcsd + a_6 \cdot mlkd + cow_m + e_{ijkm} \quad [1]$$

where Y_{ijkm} = the first-lactation record (BCS, CI, DFS, NINS, NR56, or MY3) of cow m (daughter) in herd-year of calving i that calved in month j whose dam was in age-class k ; HY_i = fixed effect of herd-year of calving interaction i , M_j = fixed effect of calving month j ($j = 1$ – 12), A_k = fixed effect of age-class of the dam k , a_1 = regression (linear and quadratic) on age at calving of the cow (age), a_2 = regression (linear) on percentage of North American Holstein genes of the cow ($phol$), a_3 = regression (linear) on MY3 of the cow ($mlkc$, for Y = BCS or fertility), a_4 = regression (linear and quadratic) on DIM of the cow (dim , for Y = BCS or MY3), a_5 = regression (linear) on dam EBV for BCS ($bcsd$, first-calving analysis) or on dam BCS ($bcsd$, second-calving analysis), a_6 = regression (linear) on dam MY3 ($mlkd$, for second-calving analysis only), cow_m = random effect of cow m (including pedigree genetic relationships among animals), and e_{ijkm} = random residual term. Each trait was analyzed separately.

The effect of interest in model [1] was the age-class of the dam (A). Days-in-milk adjusted MY3 of the cow (daughter) was included in the analysis of BCS and fertility to assess the effect of dam age on these traits for constant milk yield. Body condition score and MY3 of the dam (each adjusted for DIM) were added to remove sources of biological variation that might have otherwise masked the age of the dam effect. Because such data were not available for first-calving analysis, the dam EBV for BCS was included as a proxy to her body condition prior to first calving. All other effects fitted in model [1] were as defined in the UK national genetic evaluation model for BCS and fertility traits (Wall et al., 2003a). Furthermore, possible genetic trends affecting the traits of analysis were accounted for by the inclusion of a cow genetic effect and pedigree information.

BCS of Dam During Gestation

Data for this exercise were the 11,269 second-calving records that were considered in the previous analysis.

These included first-lactation BCS, CI, DFS, NINS, NR56, and MY3 records of dams and respective daughters from the dams' second calvings.

Each cow in the data had a single BCS record. To predict BCS during lactation and gestation, individual cow BCS records were fitted in a random regression model including DIM-adjusted MY3 and DIM when BCS was recorded. The latter was modeled with a fourth-order Legendre polynomial for the fixed curve and a second-order Legendre polynomial for the random deviation of individual cows from the fixed curve. Different fixed curves were calculated for each of the 3 age at first calving classes: early (18–23 mo), intermediate (24–29 mo), and late (30–36 mo) calvings. Cow solutions were obtained by adding the individual random effect to the corresponding fixed curve solution. This model allowed the prediction of adjusted cow BCS across a time trajectory, defined here as d 4 to 400 postpartum. A similar approach to analyzing single records per animal was proposed by Tsuruta et al. (2004). Cow solutions were subsequently de-regressed by first subtracting the appropriate fixed curve solution, then dividing by the estimated reliability and, finally, adding back the fixed curve solution (Wall et al., 2003b). For each cow, de-regressed BCS values corresponding to the last day of each month of gestation were kept.

The entire process was repeated with the analysis of individual cow BCS as single measures with a model including DIM-adjusted MY3, DIM when BCS was recorded, and cow (random). Cow solutions were de-regressed by dividing by their respective reliabilities.

The above exercise involved all cows in the data. Dams with offspring with records in the data set were matched to their own de-regressed BCS solutions. The effect of BCS of the dam on daughter performance was then assessed with the use of the following model:

$$Y_{ijm} = HY_i + M_j + a_1 \cdot age + a_2 \cdot phol + a_3 \cdot mlkc + a_4 \cdot dim + a_5 \cdot bcsc + a_6 \cdot bcsd + cow_m + e_{ijm} \quad [2]$$

where Y_{ijm} = the first lactation record (BCS, CI, DFS, NINS, NR56, or MY3) of cow m (daughter) in herd-year of calving i that calved in month j , a_5 = regression (linear) on BCS of the cow ($bcsc$, for Y = MY3 or fertility), a_6 = regression (linear and quadratic) on de-regressed solutions for BCS of the dam ($bcsd$); HY_i , M_j , a_1 , a_2 , a_3 , a_4 , cow_m , and e_{ijm} are defined as in model [1].

The regression of interest in model [2] was that of cow (daughter) trait on BCS of the dam (a_6). The latter were de-regressed cow effect solutions either from the single measure analysis or for mo 1 to 9 of gestation

from fitting a random regression model. In the latter case, 9 consecutive analyses took place for each trait.

In addition, changes in de-regressed dam BCS during gestation were considered as independent variables in model [2] to assess their effect on offspring performance. Changes were expressed either as differences of BCS on each gestation month (1 to 9) from BCS on the day of conception or as regressions of monthly BCS on time. The latter represents the average estimated BCS change during gestation. When model [2] included a BCS change effect, dam BCS level corresponding to day of conception was also fitted. Thus, the effect of BCS change during gestation was assessed for constant BCS level at the onset of gestation.

Body condition score (adjusted for DIM) of the cow (daughter) was included in the analysis of MY3 and fertility to account for the additive genetic BCS effect the dam directly transmits to her daughter and the additive genetic correlation among traits. Hence, the marginal effect estimated for BCS of the dam would describe the noninherited maternal uterine effect associated with her energy level during gestation. In the analysis of BCS of the cow, the effect of BCS of the dam would be a combination of additive genetic and prenatal maternal components.

Milk Yield of Dam During Lactation

For the purposes of this exercise, permanent environment solutions for all cows were obtained from the official UK national genetic evaluation for milk yield. The latter is calculated with a random regression model analysis of repeated test-day records of the first 3 lactations (Mrode et al., 2005). Permanent environment solutions for milk yield represent the noninherited proportion of variation during a cow's lactation and were used here to describe maternal environment.

The permanent environment solutions for milk yield on the last day of each month of lactation were extracted for all cows with at least 10 test-day records in the official analysis that also had daughters with validated fertility data. These monthly dam permanent environment solutions were then matched with their daughters' first-lactation BCS, fertility, and MY3 data. A total of 19,922 records was considered for this analysis. The effect of the dam's permanent environment solution for milk yield on cow (daughter) BCS, fertility, and MY3 was assessed using the following model:

$$Y_{ijlm} = HY_i + M_j + a_1 \cdot age + a_2 \cdot phol + a_3 \cdot mlkc [3] \\ + a_4 \cdot dim + a_5 \cdot mlkd + lcd_l + cow_m + e_{ijlm}$$

where Y_{ijlm} = the first-lactation record (BCS, CI, DFS, NINS, NR56, or MY3) of cow m (daughter) in herd-year

of calving i that calved in month j , lcd_l = fixed effect of l th lactation of the dam leading to the birth of cow m ($l = 1$ to 3), a_5 = linear regression on monthly permanent environment solution for milk yield in l th lactation of the dam ($mlkd$); HY_i , M_j , a_1 , a_2 , a_3 , a_4 , cow_m , and e_{ijlm} are defined as in model [1].

Monthly dam permanent environment solutions for milk yield were also matched with their daughters' 305-d milk, fat, and protein yield records. A total of 43,395 records of 19,922 daughters in their first 3 lactations were considered for this analysis. The effect of the dam permanent environment solution for milk yield on daughter 305-d yield was assessed using the following model:

$$Y_{ijklm} = (HY_i + M_j + a_1 \cdot age + a_5 \cdot mlkd)_k [4] \\ + a_2 \cdot phol + lcd_l + cow_m + pe_m + e_{ijklm}$$

where Y_{ijklm} = the record (305-d milk, fat, or protein yield) of cow m (daughter) in lactation k in herd-year of calving i that calved in month j , k = fixed effect of lactation of cow m ($k = 1$ to 3), pe_m = permanent environment associated with cow m ; HY_i , M_j , a_1 , a_2 , a_5 , lcd_l , cow_m , and e_{ijklm} are as defined in model [3].

The regression of interest in models [3] and [4] was that of cow (daughter) performance (BCS, fertility, MY3, or 305-d yield) on milk yield of the dam (a_5). The latter were permanent environment solutions for milk yield of the dam, for mo 1 to 10 of her lactation. Their impact was assessed in 10 consecutive analyses for each trait. In the case of 305-d daughter yield, separate coefficients were calculated for each of the 3 daughter lactations. The estimated effects represented the noninherited maternal effect associated with milk production during the dam's lactation. Because permanent environment solutions were available only for the first 305 d of lactation, the full gestation of the dam could not be modeled; therefore, associations with milk yield of the dam during gestation were not made.

Variance Due to the Dam

Data for this exercise were obtained from the UK national fertility database comprising first-lactation individual cow records on CI, DFS, NR56, NINS, BCS, and MY3, as described previously. Only dams with multiple daughters having validated fertility records were kept. This data structure ensures proper estimation of variance components including maternal effects (Maniatis and Pollott, 2003). A total of 19,623 cow records from 7,340 dams were analyzed.

The following model was used to estimate variance components:

Table 2. Effect of maternal age at first calving (SE in parentheses), expressed as deviation from the early calving class (18–23 mo), on first-lactation cow performance

Trait ¹	Age class of the dam			
	24–29 mo	<i>P</i> -value	30–36 mo	<i>P</i> -value
BCS	–0.15 (0.05)	0.00*	–0.31 (0.06)	0.00*
CI	–2.11 (1.88)	0.26	1.11 (2.09)	0.59
DFS	0.16 (1.03)	0.88	2.98 (1.15)	0.01*
NINS	–0.10 (0.04)	0.01*	–0.12 (0.04)	0.00*
NR56 ²	0.04 (0.02)	0.02*	0.05 (0.02)	0.01*
MY3	–0.52 (0.18)	0.00*	–1.18 (0.20)	0.00*

¹CI = calving interval; DFS = interval from calving to first service; NINS = number of inseminations per conception; NR56 = nonreturn rate 56 d post-first insemination; MY3 = daily milk yield on third test-day.

²0 = cow returned to service within 56 d.

*Significant at *P* = 0.05.

$$Y_{ijkm} = HY_i + M_j + a_1 \cdot age + a_2 \cdot phol + a_3 \cdot mlkc + a_4 \cdot dim + cow_m + dam_k + e_{ijkm} \quad [5]$$

where Y_{ijkm} = the first-lactation record (BCS, CI, DFS, NINS, NR56, or MY3) of cow m (daughter) in herd-year of calving i that calved in month j , dam_k = the random genetic effect of the dam of cow (including genetic relationships among animals); HY_i , M_j , a_1 , a_2 , a_3 , a_4 , cow_m , and e_{ijkm} are defined as in model [1].

In model [5], cow represented the direct additive genetic effect and dam was the overall maternal genetic effect. The latter includes both prenatal uterine and cytoplasmic components and might be thought of as any maternal contribution beyond that of the nuclear genome. The percentage of total phenotypic variance accounted for by the maternal effect would determine its importance for the traits in question. Efforts to include a direct by maternal interaction effect were computationally unsuccessful.

RESULTS AND DISCUSSION

Age of Dam at Calving

Age at calving indicates the stage of a pregnant cow's development and may be associated with the proportion of nutrients expended during gestation to support her own growth vs. development of the fetus.

The effect of maternal age at first and second calving on first-lactation daughter performance is shown in Tables 2 and 3, respectively. In both cases, the solution of the first class (early calvings) was set to zero and the effects of the other class solutions were expressed as deviations from the first. All other fixed effects included in model [1], representing sources of systematic variation, were statistically significant (*P* < 0.05). Some first-

calving data examples are presented here to illustrate the point. Regression coefficients for percentage of North American Holstein genes were –0.003 (±0.001), 0.092 (±0.006) kg, 0.171 (±0.051) d, 0.081 (±0.031) d, 0.002 (±0.001), and –0.0009 (±0.0004) for BCS, MY3, CI, DFS, NINS, and NR56, respectively. This suggests that an increase in the percentage of North American Holstein genes was associated with improved milk production but slightly compromised BCS and fertility. Similarly, the regression on cow MY3 that had been included in the analysis of BCS and fertility to ensure assessment of the effect of dam age for constant milk yield, was –0.012 (±0.002) for BCS, 0.560 (±0.085) d for CI, 0.412 (±0.045) d for DFS, 0.007 (±0.002) for NINS, and –0.003 (±0.001) for NR56.

The age of the dam at her first calving had a significant (*P* < 0.05) effect on daughter BCS, DFS, NINS, NR56, and MY3 (Table 2). Daughters of older dams had lower BCS, paradoxically produced less daily milk, and needed more days to first service. In fact, daughters from late calvings (30–36 mo) had 0.31 lower BCS (7% of the mean), produced 1.18 kg less milk (4.5% of the mean), and had their first service almost 3 d (3.4% of the mean) later than daughters from early calvings (18–23 mo). On the other hand, cows whose dams calved at intermediate or older age needed fewer inseminations per conception and had fewer returns to estrus (i.e., a higher proportion conceived in first insemination). Thus, the nonreturn rate of daughters from the 24–29 mo and the 30–36 mo maternal age class was 6 and 7.5% higher than those from the early calving class (18–23 mo), respectively. Furthermore, the later calving groups needed 6 to 7% fewer inseminations per conception compared with the early group. The opposing combined effects on NR56, NINS, and DFS resulted in nonsignificant differences between CI of daughters from different maternal age classes.

The significance of this result was corroborated by a side analysis of the same data using model [1], except that age of dam was now fitted as a linear and quadratic regression instead of a class variable. Significantly (*P* < 0.05) negative linear regressions were observed for BCS, NINS, and MY3, and positive for DFS and NR56. The quadratic regression was significant only for NINS and NR56.

A first-calving cow is frequently a growing cow (Coffey et al., 2006). Therefore, she requires nutrients for both maintenance and her own body development during first lactation. During the pregnancy period leading to this first calving, the fetus may face intense competition for nutrients from its mother's own metabolic needs. As a consequence, early-calving cows may produce calves with difficulties at conceiving as first-lactation cows, as manifested by the adverse impact on NINS and NR56.

Table 3. Effect of maternal age at second calving (SE in parentheses), expressed as deviation from the early calving class (30–35 mo), on first-lactation cow performance

Trait ¹	Age class of the dam					
	36–41 mo	<i>P</i> -value	42–46 mo	<i>P</i> -value	47–55 mo	<i>P</i> -value
BCS	–0.07 (0.05)	0.14	–0.17 (0.06)	0.00*	–0.07 (0.08)	0.40
CI	5.93 (1.75)	0.00*	9.33 (1.99)	0.00*	13.15 (2.85)	0.00*
DFS	2.49 (0.96)	0.01*	4.47 (1.09)	0.00*	7.95 (1.59)	0.00*
NINS	0.08 (0.04)	0.03*	0.09 (0.04)	0.02*	0.12 (0.06)	0.05*
NR56 ²	0.00 (0.01)	0.86	0.00 (0.02)	0.88	–0.01 (0.02)	0.71
MY3	–0.64 (0.16)	0.00*	–1.16 (0.18)	0.00*	–1.56 (0.26)	0.00*

¹CI = calving interval; DFS = interval from calving to first service; NINS = number of inseminations per conception; NR56 = nonreturn rate 56 d post first insemination; MY3 = daily milk yield on third test-day.

²0 = cow returned to service within 56 d.

*Significant at *P* = 0.05.

This is a marginal effect adjusted for the cow's own age at calving. These cows seem to mature early, exhibiting the characteristics of high-producing Holsteins, but they can not conceive as easily as cows born to older first-calving dams.

The age of the dam at her second calving had a significant (*P* < 0.05) effect on all daughter traits except NR56 (Table 3). Clear trends were observed for increasing CI, DFS, and NINS and decreasing MY3 with the age of the dam. In general, daughters from late-calving dams had longer intervals from calving to first service, meaning they delayed showing evident estrus by up to 8 d (9% of the mean) and needed as many as 7% more inseminations per conception; consequently, they had longer CI. In addition, they produced nearly 6% less MY3 than their early calving (30–35 mo) counterparts. They also had lower BCS, although the effect was statistically significant (*P* < 0.05) only in the case of intermediate-late calvings (42–46 mo).

Fitting age at second calving as a linear and quadratic regression instead of a class variable supported these findings as the linear regression was significantly (*P* < 0.05) negative (unfavorable) for BCS and MY3 and positive (unfavorable) for CI, DFS, and NINS. The quadratic regression was significant only for CI.

Second-calving Holsteins are usually animals that have completed their growth phase. As cows age, the frequency of chromosomal abnormalities increases, with consequences for the offspring's productive and reproductive life. Fuerst-Waltl et al. (2004) reported decreasing milk production, nonreturn rate, and longevity with maternal age in Austrian dual-purpose Simmental cows. Admittedly, their data spanned a wider range of ages, reaching a maximum of 16 yr compared with 4.5 yr in the present study. However, Simmentals mature later than Holsteins. Furthermore, the effect was evident even for early age classes in the Fuerst-Waltl et al. (2004) study; for a maternal age class of 4 to 5 yr, first-lactation ECM yield was reduced by

approximately 1% (*P* < 0.01) and nonreturn rate decreased by 3% (*P* = 0.24) compared with a maternal age class of 2 to 3 yr (Fuerst-Waltl et al., 2004). No other similar studies on dairy cattle were found in the literature. Wang and vom Saal (2000) reported delayed puberty in mice born to older dams.

BCS of Dam During Gestation

The BCS of a pregnant cow is associated with the amount of energy available to her to sustain growth, maintenance, milk production, and fetal development. In this respect, a cow's BCS level and change during gestation can be associated with the proportion of energy expended to cover the needs of the embryo, which can potentially affect the latter's future performance as a milk-producing cow.

In the present study, the effect of dam BCS, derived from a single measure analysis, on first-lactation daughter performance is shown in Table 4. All other fixed effects included in model [2] were statistically significant (*P* < 0.05). For example, regression coefficients for the percentage of North American Holstein

Table 4. Effect of maternal BCS, derived from single measure analysis, on first-lactation cow performance (SE in parentheses)

Trait ¹	Linear regression		Quadratic regression	
	regression	<i>P</i> -value	regression	<i>P</i> -value
BCS	0.08 (0.01)	0.00*	0.01 (0.00)	0.03*
CI	–0.78 (0.46)	0.09	0.07 (0.19)	0.72
DFS	–0.30 (0.23)	0.19	–0.06 (0.09)	0.53
NINS	–0.03 (0.01)	0.00*	0.01 (0.00)	0.10
NR56 ²	0.01 (0.00)	0.00*	0.00 (0.00)	0.44
MY3	–0.09 (0.04)	0.01*	0.01 (0.01)	0.66

¹CI = calving interval; DFS = interval from calving to first service; NINS = number of inseminations per conception; NR56 = nonreturn rate 56 d post first insemination; MY3 = daily milk yield on third test-day.

²0 = cow returned to service within 56 d.

*Significant at *P* = 0.05.

genes were $-0.007 (\pm 0.003)$, $0.023 (\pm 0.008)$ kg, $0.134 (\pm 0.059)$ d, $0.039 (\pm 0.020)$ d, $0.0036 (\pm 0.0017)$, and $-0.0007 (\pm 0.0004)$ for BCS, MY3, CI, DFS, NINS, and NR56, respectively. Furthermore, the regression on cow MY3 was $-0.046 (\pm 0.004)$ for BCS, $0.591 (\pm 0.139)$ d for CI, $0.291 (\pm 0.071)$ d for DFS, $0.007 (\pm 0.003)$ for NINS, and $-0.0009 (\pm 0.0004)$ for NR56. These effect solutions, which are based on the analysis of cow records from second dam calvings, were similar to those from model [1], as reported earlier, pertaining to cow records from the first calvings of their dams.

The effect of dam BCS on daughter BCS was positive and, to a certain extent, is affected by the additive genetic heritability. The analysis of the other traits, however, had accounted for BCS of the daughter and hence for the additive genetic correlation between these traits and BCS. Therefore, the estimated effect of dam BCS on daughter fertility and MY3 was free from any direct genetic component and reflected the prenatal maternal environment as described by the body energy content and body condition of the dam. This effect was significantly ($P < 0.05$) negative on NINS and MY3, and positive on NR56 (Table 4). This means that dams offering a high-energy uterine environment to the fetus had offspring with improved fertility but slightly reduced test-day milk yield. A 1-point increase in maternal BCS level (on the 1 to 9 scale) would result in a 1% higher nonreturn rate, 0.03 fewer inseminations per conception, and 90 g less daily milk produced by the offspring. Higher dam BCS would also shorten CI and DFS but this result was not statistically significant in the present study ($P = 0.09$ and $P = 0.19$, respectively).

The effect of BCS of the dam at different stages of gestation on daughter NINS, NR56, and MY3 is shown in Figure 1. These 3 traits were significantly affected by the prenatal environment expressed by the overall body condition of the dam (Table 4). Results presented in Figure 1 are from 10 separate analyses considering predicted dam BCS at the day of conception and then at 30-d intervals corresponding to the 9 mo of gestation. The effect was more pronounced during the second and third trimesters of gestation. This may be associated with critical phases in the development of the embryo. Thus, cows that maintain high BCS in mid to late gestation appear to produce offspring with improved fertility but slightly reduced test-day milk. The opposing signs for these effects are probably associated with the antagonistic relationship between milk yield and fertility. Furthermore, MY3 was evidently more affected by dam BCS during the last 2 mo of gestation (Figure 1). The latter coincides with the cow's dry period. It can be speculated that cows that build good body condition during this period are likely to have offspring more

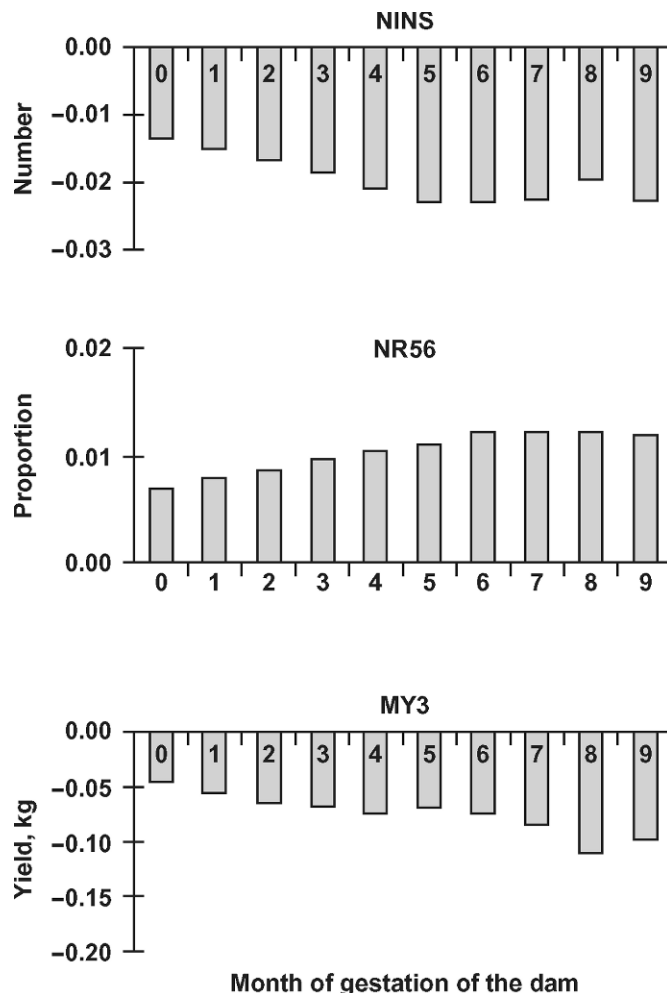


Figure 1. Effect of maternal BCS in different months of gestation of the dam on first-lactation cow performance. NINS = number of inseminations per conception; NR56 = nonreturn rate 56 d post first insemination (0 = cow returned to service); and MY3 = daily milk yield on third test-day.

inclined to reserve energy for the benefit of body condition and fertility rather than expend it to produce milk.

Changes in dam BCS during gestation had no significant effect ($P > 0.05$) on daughter performance. Results were the same whether changes had been expressed as differences of BCS on each gestation month (1 to 9) from BCS on the day of conception or as regressions of monthly BCS on time. On average, dam BCS increased by 0.04 (standard deviation = 0.13) points (de-regressed solutions) during gestation. The effect of this change was adjusted for BCS at the onset of gestation so it was assessed for a constant level of BCS for all cows. The most notable findings here were an increase of daughter BCS by $0.79 (\pm 0.48; P = 0.10)$ for each 1-point increase in maternal BCS gain and a corresponding daily milk reduction of $2.31 \text{ kg } (\pm 1.50; P =$

0.12). A 1-point increase in BCS gain is only a theoretical figure, as in our data the absolute maximum change was 0.45 points. These results suggest that dams with above average BCS gains during gestation may produce better conditioned daughters that yield slightly less daily milk.

Milk Yield of Dam During Lactation

Impact on Daughter First-Lactation Traits. Milk yield is the key competitor to the fetus for nutrients during gestation and may influence the latter's development indirectly in early gestation, when fetal nutrient requirements are low, and then directly later in gestation when they are high.

The effect of milk yield of the dam, expressed here as monthly permanent environment solutions, on first-lactation daughter BCS, fertility, and MY3 was nonsignificant ($P > 0.05$) in all cases. This means that maternal effects (as measured by permanent environmental solutions for milk production) during a dam's lactation do not have an impact on first-lactation performance of the offspring that was born during that lactation. In the present study, a cow's lactation was defined by the first 305 d. This partially overlaps with her gestation (average number of days open in the data was 112) meaning that the full gestation could not be modeled. However, our results suggest that a maternal environment defined by high milk yield of the dam during conception and the early stages of gestation does not seem to affect future offspring's first-lactation BCS, fertility, and MY3.

In the first instance, permanent environment of the dam during any lactation (first, second, or third) leading to the birth of a particular offspring was considered. It could be argued, however, that animals are still growing during their first lactation, whereas in lactations 2 and 3 they are closer to mature size; therefore, animals might exhibit different behavior regarding partitioning of nutrients and energy in first vs. later lactations. To test this, the entire exercise was repeated considering maternal yield (permanent environment solutions) from the dam's first lactation only; results (not shown), however, did not change. In all cases, the impact of maternal yield on first-lactation daughter BCS, fertility, and MY3 was nonsignificant ($P > 0.05$).

Impact on Daughter Yield in the First Three Lactations. The overall effect of dam milk yield, expressed as monthly permanent environment solutions, on daughter 305-d yield in their first 3 lactations was significant ($P < 0.05$) in all cases. Figure 2 depicts the linear regressions of daughter 305-d yield on dam milk permanent environment per month of dam's lactation, emanating from 10 consecutive analyses with model

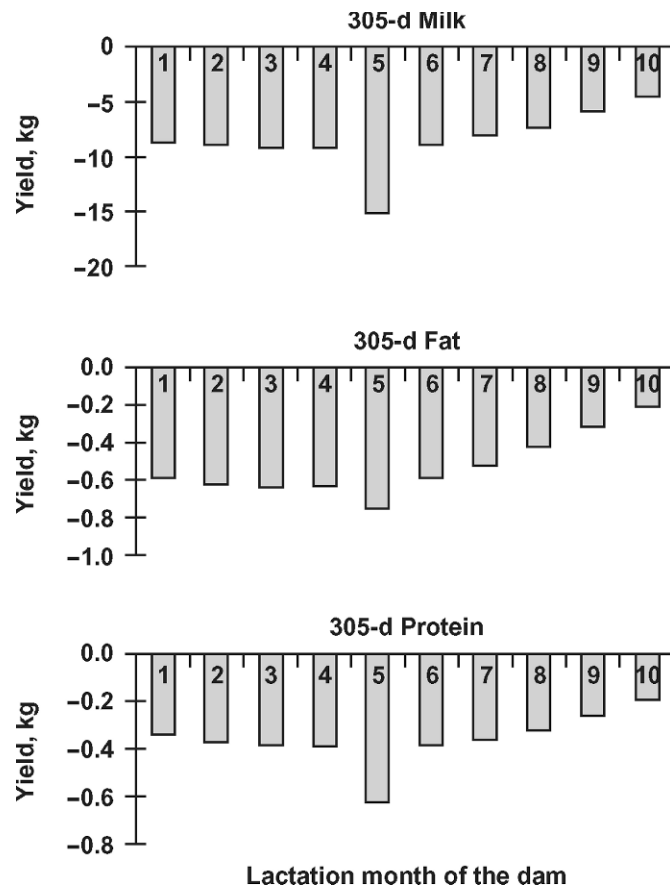


Figure 2. Effect of maternal milk yield in different months of lactation of the dam on daughter 305-d yield in the latter's first 3 lactations.

[4]. This effect is pooled across the daughters' 3 lactations. In general, increasing maternal milk yield was associated with decreasing daughter yield; month 5 of lactation of the dam had the most pronounced effect (Figure 2). However, although significant, this effect was practically negligible because it amounted to a maximum of 0.17, 0.23, and 0.22% of the average 305-d milk, fat, and protein yields, respectively.

Looking at daughter yield in each lactation separately, the effect of maternal yield followed the pattern of Figure 2 in all cases; however, the effect was significant ($P < 0.05$) for lactations 2 and 3 but not ($P > 0.05$) for lactation 1. The latter is consistent with our results regarding MY3. It may not be immediately obvious why such an effect is only significant on greater-than-first-lactation daughter production. Possibly cows that have completed their own growth are more responsive to other factors that may prohibit full expression of their producing potential.

In general, our results suggest that a favorable maternal yield environment appears to have a very small

Table 5. Proportion of total phenotypic variance accounted for by direct additive and maternal genetic effects for first-lactation cow performance (SE in parentheses)

Trait ¹	Direct	Maternal
BCS	0.18 (0.03)*	0.029 (0.027)
CI	0.03 (0.01)*	0.014 (0.006)*
DFS	0.04 (0.01)*	0.024 (0.015)
NINS	0.02 (0.01)*	0.009 (0.006)
NR56	0.01 (0.00)*	0.011 (0.005)*
MY3	0.27 (0.02)*	0.003 (0.010)

¹CI = calving interval; DFS = interval from calving to first service; NINS = number of inseminations per conception; NR56 = nonreturn rate 56 d post first insemination; MY3 = daily milk yield on third test-day.

*Significant at $P = 0.05$.

(<0.3% of the mean) adverse effect on future daughter 305-d production. Because this definition of maternal yield does not include any genetic effects, it can be entirely associated with the maternal environment during lactation, which coincides with the time the offspring was conceived and in early gestation. Negative environmental correlations between dam and offspring performance are not uncommon in livestock (Bijma, 2006). Furthermore, they may often affect the estimation of additive genetic correlation between direct and maternal effects (Bijma, 2006). Although there are studies of the latter in dairy cattle (e.g., Schutz et al., 1992; Albuquerque et al., 1998), reports on nongenetic relationships are largely missing. Van Vleck and Bradford (1965) suggested that they are probably very small, supporting results from the present study. In beef cattle, antagonistic environmental associations between dam and offspring have been reported for some growth traits (Cantet et al., 1988; Dodenhoff et al., 1998).

In this exercise, the effect of milk yield of the dam was described by permanent environment solutions from the UK national genetic evaluation. Such solutions were available throughout the lactation of each cow. Therefore, it was possible to assess the impact of this effect at different stages of lactation. Temporary environmental effects specific to the time when a dam is bearing her offspring might also be important but were not considered in the present study.

Variance Due to the Dam

Table 5 shows the proportion of total phenotypic variance of first-lactation traits accounted for by direct additive and maternal genetic effects. The former, equivalent to narrow sense heritability, was 0.18 and 0.27 for BCS and MY3, respectively, whereas it ranged between 0.01 and 0.04 for the 4 fertility traits. All estimates were significantly greater than zero ($P < 0.05$) and consistent

with those used in the UK national genetic evaluation for fertility (Wall et al., 2003a).

Maternal genetic effects accounted for a relatively small proportion of variance for each trait. Exceptions were the 2 significant ($P < 0.05$) estimates derived for CI (1.4%) and NR56 (1.1%). These estimates reflect the combined effects of uterine environment, cytoplasmic inheritance, egg quality, and fetus survival. For the 2 lowly heritable traits, these are considerable proportions. Estimates from the present study are very similar to those reported by A.-Ranberg et al. (2003; 1.2% for NR56), slightly higher than those by Jansen (1986; 0.7% for NR56) and lower than those of Jamrozik et al. (2005; 4 to 6% for similar fertility traits).

Maternal genetic effects accounted for just 0.3% of the total variation of MY3 and it was nonsignificant ($P = 0.10$). This is lower than the 1.1% reported by Albuquerque et al. (1998) for 305-d lactation milk yield.

CONCLUSIONS

This study set out to investigate the impact of various maternal effects on future offspring performance. Based on results presented here, the following conclusions may be drawn.

Optimal first-calving age is between 24 and 29 mo. Ensuing progeny are then expected to have a better balance of production, BCS, and fertility profiles. On the other hand, calving at an earlier age would produce high-yielding offspring that may later experience difficulties in conceiving as first-lactation cows.

The interval between first and second calving should decrease. Offspring resulting from early second calvings would be associated with increased production and improved BCS and fertility.

A dam's BCS during gestation has an impact on the calf's future performance. It is important to avoid BCS losses of the dam especially during the second and third trimester of gestation. Appropriate nutritional strategies at late lactation and the dry period become crucial factors in this respect.

Continuing selection for milk production may be linked to a slightly adverse cross-generational environmental effect, meaning that production of daughters of high-yielding dams can be compromised. However, the very small magnitude of this effect is not expected to seriously influence milk selection and genetic improvement programs.

Finally, maternal genetic effects seem to account for a significant proportion of the total phenotypic variance of calving interval and nonreturn rate. Including such effects in genetic evaluation models is recommended because it would improve variance partitioning and breeding value estimation.

ACKNOWLEDGMENTS

This work was partly financed by Avoncroft Sires Ltd., BOCM Pauls Ltd., CIS, Cogent, Dartington Cattle Breeding Trust, Genus Breeding Ltd., Holstein UK, National Milk Records plc, the Royal Society for the Prevention of Cruelty to Animals, and the UK Department for Environment Food and Rural Affairs, in the Sustainable Livestock Production LINK program. The work was based on data collected under a grant from the Scottish Executive Environment and Rural Affairs Department. Useful discussions with Geoff Pollott and Eileen Wall are gratefully acknowledged. Many thanks also to Raphael Mrode for making cow permanent environment solutions available from the UK national genetic evaluation system.

REFERENCES

- Albuquerque, L. G., J. F. Keown, and L. D. Van Vleck. 1998. Variances of direct genetic effects, maternal genetic effects, and cytoplasmic inheritance effects for milk yield, fat yield, and fat percentage. *J. Dairy Sci.* 81:544–549.
- A.-Ranberg, I. M., B. Heringstad, G. Klemetsdal, M. Svendsen, and T. Steine. 2003. Heifer fertility in Norwegian dairy cattle: Variance components and genetic change. *J. Dairy Sci.* 86:2706–2714.
- Barker, D. J. P. 1992. Impact of diet on critical events in development: The effect of nutrition of the fetus and neonate on cardiovascular disease in adult life. *Proc. Nutr. Soc.* 51:135–144.
- Bijma, P. 2006. Estimating maternal genetic effects in livestock. *J. Anim. Sci.* 84:800–806.
- Borwick, S. C., S. M. Rhind, S. R. McMillen, and P. A. Racey. 1997. Effect of undernutrition of ewes from the time of mating on fetal ovarian development in mid gestation. *Reprod. Fertil. Dev.* 9:711–715.
- Brotherstone, S. 1994. Genetic and phenotypic correlations between linear type traits and production traits in Holstein-Friesian dairy cattle. *Anim. Prod.* 59:183–187.
- Cantet, R. J. C., D. D. Kress, D. C. Anderson, D. E. Doornbos, P. J. Burfening, and R. L. Blackwell. 1988. Direct and maternal variances and covariances and maternal phenotypic effects on preweaning growth of beef cattle. *J. Anim. Sci.* 66:648–660.
- Coffey, M. P., J. Hickey, and S. Brotherstone. 2006. Genetic aspects of growth of Holstein-Friesian dairy cows from birth to maturity. *J. Dairy Sci.* 89:322–329.
- Cowley, D. E., D. Pomp, W. R. Atchley, E. J. Eisen, and D. Hawkins-Brown. 1989. The impact of maternal uterine genotype on postnatal growth and adult body size in mice. *Genetics* 122:193–203.
- Dodenhoff, J., L. D. Van Vleck, S. D. Kachman, and R. M. Koch. 1998. Parameter estimates for direct, maternal, and grandmaternal genetic effects for birth weight and weaning weight in Hereford cattle. *J. Anim. Sci.* 76:2521–2527.
- Drake, A. J., and B. R. Walker. 2004. The intergenerational effects of fetal programming: non-genomic mechanisms for the inheritance of low birth weight and cardiovascular risk. *J. Endocrinol.* 180:1–16.
- Fuerst-Waltl, B., A. Reichl, C. Fuerst, R. Baumung, and J. Sölkner. 2004. Effect of maternal age on milk production traits, fertility, and longevity in cattle. *J. Dairy Sci.* 87:2293–2298.
- Gilmour, A. R., B. J. Gogel, B. R. Cullis, S. J. Welham, and R. Thompson. 2002. ASREML User Guide. Release 1.0 VSN International Ltd., Hemel Hempstead, UK.
- Gunn, R. G., D. A. Sim, and E. A. Hunter. 1995. Effects of nutrition in utero and in early life on the subsequent lifetime and reproductive performance of Scottish Blackface ewes in two management systems. *Anim. Sci.* 60:223–230.
- Jamrozik, J., J. Fatehi, G. J. Kistemaker, and L. R. Schaeffer. 2005. Estimates of genetic parameters for Canadian Holstein female reproduction traits. *J. Dairy Sci.* 88:2199–2208.
- Jansen, J. 1986. Direct and maternal genetic parameters of fertility traits in Friesian cattle. *Livest. Prod. Sci.* 15:153–164.
- Jones, H. E., I. M. S. White, and S. Brotherstone. 1999. Genetic evaluation of Holstein Friesian sires for daughter condition-score changes using a random regression model. *Anim. Sci.* 68:467–475.
- Kadarmideen, H. N., and M. P. Coffey. 2001. Quality and validation of insemination data for national genetic evaluations for dairy cow fertility in the United Kingdom. *Proc. Annu. Interbull Mtg., Budapest, Hungary. Interbull Bull.* 27:133–138.
- Maniatis, N., and G. E. Pollott. 2003. The impact of data structure on genetic (co)variance components of early growth in sheep, estimated using an animal model with maternal effects. *J. Anim. Sci.* 81:101–108.
- Mousseau, T. A., and C. W. Fox. 1998. Maternal Effects as Adaptations. Oxford Univ. Press, Oxford, UK.
- Mrode, R., S. Brotherstone, I. White, G. Swanson, M. Coffey, H. Jones, and R. Thompson. 2005. Random regression model for the genetic evaluation of production traits of dairy cattle in the UK. *Proc. Annu. Interbull Mtg., Uppsala, Sweden. Interbull Bull.* 33:211–214.
- Pryce, J. E., G. Simm, and J. J. Robinson. 2002. Effects of selection for production and maternal diet on maiden dairy heifer fertility. *Anim. Sci.* 74:415–421.
- Rhees, B. K., C. A. Ernst, C. H. Miao, and W. R. Atchley. 1999. Uterine and postnatal maternal effects in mice selected for differential rate of early development. *Genetics* 153:905–917.
- Roseboom, T. J., J. H. P. van der Meulen, C. Osmond, D. J. P. Barker, A. C. J. Ravelli, J. M. Schroeder-Tanka, G. A. van Montfrans, R. P. J. Michels, and O. P. Bleker. 2000. Coronary heart disease after prenatal exposure to the Dutch famine, 1944–45. *Heart* 84:595–598.
- Rutledge, J. J., O. W. Robinson, E. J. Eisen, and J. E. Legates. 1972. Dynamics of genetic and maternal effects in mice. *J. Anim. Sci.* 35:911–918.
- Schutz, M. M., A. E. Freeman, D. C. Beitz, and J. E. Mayfield. 1992. The importance of maternal lineage on milk yield traits of dairy cattle. *J. Dairy Sci.* 75:1331–1341.
- Tsuruta, S., I. Misztal, T. J. Lawlor, and L. Klei. 2004. Modeling final scores in US Holsteins as a function of year of classification using a random regression model. *Livest. Prod. Sci.* 91:199–207.
- Van Vleck, L. D., and G. E. Bradford. 1965. Genetic covariances among relatives for dairy lactation records. *Genetics* 52:385–390.
- Wall, E., S. Brotherstone, J. A. Woolliams, G. Banos, and M. P. Coffey. 2003a. Genetic evaluation of fertility using direct and correlated traits. *J. Dairy Sci.* 86:4093–4102.
- Wall, E., V. E. Olori, M. P. Coffey, and S. Brotherstone. 2003b. Prediction of UK fertility proofs for foreign bulls. *Proc. Annu. Interbull Mtg., Rome, Italy. Interbull Bull.* 31:60–64.
- Wang, M. H., and F. S. vom Saal. 2000. Maternal age and traits in offspring. *Nature* 407:469–470.